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The Omo I hominin clavicle: Archaic or modern?

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ABSTRACT

Assessment of clavicular curvatures projected onto two perpendicular planes to decompose the three dimensional shape into cranial and dorsal primary curvatures has shown that two morphological groups of clavicle exist within the genus *Homo*. The first one includes all species from *Homo habilis* to Neandertals, while the second includes only Upper Paleolithic remains and more recent modern humans. These morphological differences are associated with different shoulder architectures. The morphology of the Omo I left clavicle is sufficiently complete to compare its curvatures to other clavicles of several species of *Homo*. Its overall morphology, assessed by its curvatures, is similar to that of Upper Paleolithic remains and modern humans, confirming the conclusions of previous descriptions of the Omo I remains in general and of its clavicles in particular.

RÉSUMÉ

La morphologie claviculaire estimée à partir des courbures, projetées sur deux plans perpendiculaires pouvant être considérés comme les plans dorsal et cranial, a montré que deux groupes de clavicules existent au sein du genre *Homo* : le premier groupe comprend toutes les espèces allant d'*Homo habilis* à Néanderthal et le second comprend les hommes du Paléolithique supérieur et modernes. Ces différences morphologiques sont en outre associées à des architectures différentes de l'épaule. La morphologie claviculaire d'Omo I gauche (la seule pratiquement complète), estimée à partir de ses courbures, est comparée avec celles d'autres restes attribuées au genre *Homo*. Par sa morphologie générale elle se révèle similaire à celle de l'homme moderne, ce qui confirme les conclusions des descriptions déjà faites des restes d'Omo I KHS en général et de sa clavicule en particulier.

Introduction

The Omo I skeleton from KHS (Kamoya's Hominid Site) constitutes the earliest fossil remains of *Homo sapiens*, with an age of 195 ± 5 ka (McDougall et al., 2005, 2008). The Omo I skeleton has been described as anatomically modern because it shares numerous cranial and postcranial characters with our own species (Day, 1969; Day and Stringer, 1991; Day et al., 1991; Pearson et al., 2008), although some histological characteristics suggest a closer resemblance to earlier species of *Homo* (Bartsiokas, 2002). As differences in clavicular morphology are associated with different shoulder architectures in the genus *Homo* (Voisin, 2004, 2006a), this paper focuses on the clavicular morphology of the Omo I skeleton.

Although clavicular morphology is a crucial element for upper-limb movements and shoulder architecture (Voisin, 2006b), little emphasis has been placed on this bone in an evolutionary context. Most work on it has been strictly anthropometric rather than evolutionary, with detailed overviews of its morphological variations within modern humans frequently provided (i.e., Broca, 1869; Parson, 1917; Kleiweg de Zwaan, 1931; Terry, 1932; Apostolakis, 1934; Olivier, 1951b,c, 1954a,b, 1955; Olivier and Carrère, 1953; Olivier et al., 1954; Olivier and Capliez, 1957; Ray, 1959; Longia et al., 1982; Jit and Kaur, 1986; Murphy, 1994). On the other hand, only a few studies have compared primate clavicles from the point of view of comparative anatomy or functional morphology, and most of these studies are relatively recent (Schultz, 1930; Olivier, 1953; Cave, 1961; Jenkins, 1974; Jenkins et al., 1978; Ljunggren, 1979; Harrington et al., 1993; Voisin, 2000, 2006b; Voisin and Balzeau, 2004). This recent development of interest in the clavicle explains in part why fossil clavicles have been so neglected and their study limited to descriptions, although some authors have tried to go further, with functional interpretations or comparison with other hominins in the search for taxonomic characters (Heim, 1982a,b; Vandermeersch and Trinkaus, 1995; Sankhyan, 1997, 2005; Voisin, 2000, 2001, 2004, 2006a).

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The aim of this study is to compare the Omo I clavicles with other clavicles of *Homo*, including *Homo habilis*, Neandertals, and recent *H. sapiens*, and to try to interpret differences and similarities from an adaptive and evolutionary perspective.

Materials and methods

The samples studied were drawn from the following fossil taxa: *H. habilis*, *H. ergaster*, *H. antecessor*, Neandertal and Upper Paleolithic remains (Table 1), and 33 clavicles of modern humans from various parts of the world (Europe, $n = 10$; Africa, $n = 7$; North America, $n = 5$; Asia $n = 7$; unknown, $n = 4$). These specimens are housed in the Laboratoire d'Anthropologie Biologique du Musée de l'Homme (Paris, France), the Institut de Paléontologie Humaine (Paris, France), and the Croatian Natural History Museum (Zagreb, Croatia). Most fossil clavicles used in this study are well preserved, even if some are eroded at their extremities; only La Chapelle-aux-Saints, Krapina 149 (right), 145 (right), 144 (right), 155 (left), 156 (left), and Qafzeh 9 (left) are not complete (Boule, 1911–1913; Vandermeersch, 1981; Radovčić et al., 1988).

Due to its complex geometry, the morphology of the clavicle was studied in regard to its curvatures. When projected onto two perpendicular planes—cranial and dorsal—the three-dimensional structure of the bone can be visualized as two basic curves (Fig. 1) in each plane. The middle arc of curvature was estimated according to Olivier's method (1951a) as the ratio between the length of the chord (h or h′, g or g′) and the height of the curvature (e or e′, f or f′) (Fig. 1). In the cranial plane, the acromial (or external) curvature is equal to e/h × 100, while the sternal (or internal) curvature is equal to f/g × 100. In the dorsal plane, the acromial (or inferior) curvature is equal to e′/h′ × 100, while the sternal (or superior) curvature is equal to f′/g′ × 100. Descriptions and distributions of these variables were computed using ViStat 6.4® (Young, 2001), and the ranges of variation are illustrated as the mean ± two standard deviations.

Table 1
Fossil clavicles studied

Upper Paleolithic	Middle Paleolithic
Anatomically modern humans	*Anatomically modern humans*
Abri Pataud (R)*	Omo I KHS (L)
Qafzeh 9 (L)	*Neandertals*
Taforalt	Régourdou (R)
Taf V-6* (*R*)	Régourdou (L)
Taf XXIII* (*L*)	Kebara 2 (R)
Taf XIX-3a* (*L*)	Kebara 2 (L)
Taf V-24* (*L*)	La Ferrassie I (R)*
Taf XI-AR* (*R*)	La Ferrassie I (L)*
Taf XVa* (*L*)	Neanderthal (R)
Taf XVc* (*L*)	Krapina 153 (L)*
Taf XVII-26* (*R*)	Krapina 142 (R)*
Taf XVIII-6* (*R*)	Krapina 143 (R)*
Taf 24-5* (*R*)	Krapina 154 (L)*
Taf XXVc* (*L*)	Krapina 145 (R)*
Taf XIIIa* (*L*)	Krapina 145 (R)*
Taf VIII-3bis* (*L*)	Krapina 155 (L)*
Taf XXVa* (*R*)	Krapina 149 (R)*
Taf IX-39* (*L*)	Krapina 144 (R)*
Taf XIIIb* (*R*)	Krapina 156 (L)*
Taf XVIIa* (*R*)	La Chapelle-aux-Saints (L)*
Taf XVI-15* (*R*)	Lower Paleolithic
Taf XVI* (*R*)	*H. antecessor*
Taf XIV* (*L*)	Gran Dolina ATD6-50 (R)
Taf XIX-3* (*R*)	*H. ergaster*
	KNM-WT 15000 (R & L)
	H. habilis
	OH 48 (L)

* Original remains; R = right; L = left.

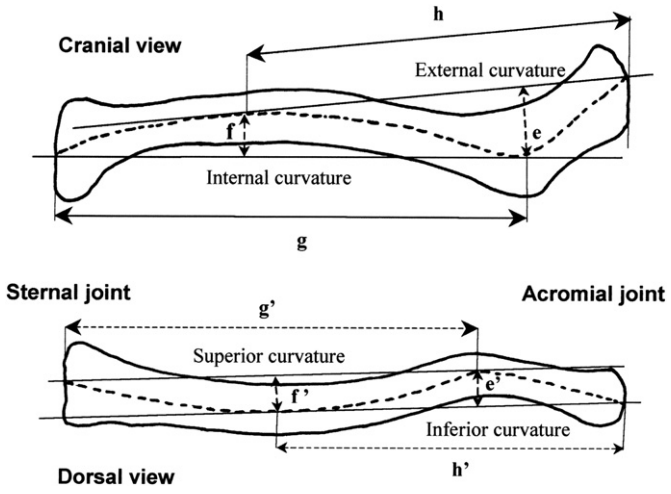

Fig. 1. Determination of clavicular curvatures on a right clavicle of *Pan troglodytes* (Olivier, 1951a).

Results

Curvatures in cranial view

In cranial view, all fossil clavicles studied here, including the left clavicle of Omo I, are distributed within the range of variation of modern humans (Fig. 2; Tables 2 and 3). This is true generally for the Neandertal clavicles, as demonstrated previously (Voisin, 2004, 2006b). However, the OH 48, KNM-WT 15000 (left), and Kebara (right) specimens exhibit a few differences from modern clavicles. Their internal curvature is more pronounced than their external one. In the case of OH 48 and Kebara (right), this morphology may be due to the loss of a large portion of their acromial extremities

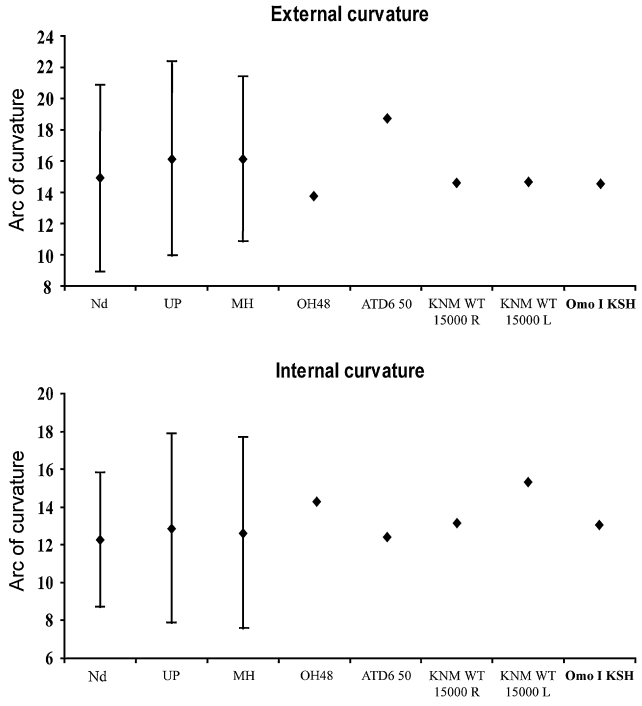

Fig. 2. Mean and range of variation of clavicular curvatures in cranial view in *H. habilis*, *H. ergaster*, *H. antecessor*, Neandertals (Nd), Upper Paleolithic (UP) remains, and modern humans (MH).

Table 2
Values of the external and internal clavicular curvatures in Upper Paleolithic and other hominin remains

Individual	Internal curvature	External curvature
Omo I KHS (L)	13.1	14.7
Upper Paleolithic		
Abri Pataud	9.7	12.1
Qafzeh 9 (L)	10.7	—
Taf V-6 (R)	16.3	19.1
Taf XXIII (L)	9.9	10.9
Taf XIX-3a (L)	10.6	14.0
Taf V-24 (L)	13.2	16.3
Taf XI-AR (R)	11.2	13.4
Taf XVa (L)	13.8	18.0
Taf XVc (L)	16.5	18.9
Taf XVII-26 (R)	12.7	19.3
Taf XVIII-6 (R)	15.0	16.3
Taf XIIIa (L)	11.4	11.9
Taf VIII-3bis (L)	13.2	16.5
Taf XXVa (R)	10.5	17.1
Taf IX-39 (L)	10.5	17.0
Taf XIIIb (R)	12.8	16.5
Taf XVIIa (R)	14.4	14.3
Taf XVI-15 (R)	8.2	13.1
Taf XVI (R)	16.8	20.8
Taf XIV (L)	12.2	16.2
Taf 24-5 (R)	11.6	14.7
Taf XIX-3 (R)	18.2	20.5
Taf XXVc (L)	14.0	20.2
Mean	**12.9**	**16.1**
Standard deviation	**2.5**	**3.1**
Neandertals		
Régourdou (R)	10.0	14.5
Régourdou (L)	11.9	13.2
Kebara (L)	11.1	16.5
Kebara (R)	11.3	9.5
La Ferrassie 1 (R)	13.2	14.2
La Ferrassie 1 (L)	12.3	17.7
Neanderthal (R)	13.2	16.7
Krapina 153 (L)	10.8	10.3
Krapina 142 (R)	17.4	16.7
Krapina 143 (R)	13.9	12.1
Krapina 154 (L).	14.1	11.4
Krapina 149 (R)	20.0	—
Krapina 145 (R)	—	11.3
Krapina 144 (R)	12.0	—
Krapina 155 (L)	18.1	—
Krapina 156 (L)	—	14.7
La Chapelle-aux-Saints (L)	—	12.2
Mean	**13.5**	**13.6**
Standard deviation	**3.0**	**2.6**
Lower Paleolithic		
KNM-WT 15000 (R)	13.1	14.6
KNM-WT 15000 (L)	15.3	14.7
ATD-6 50 (R)	12.4	18.7
OH 48 (L)	14.3	13.8

Dash indicates that the presence of a curvature is impossible to assess because of the incompleteness of the fossil.

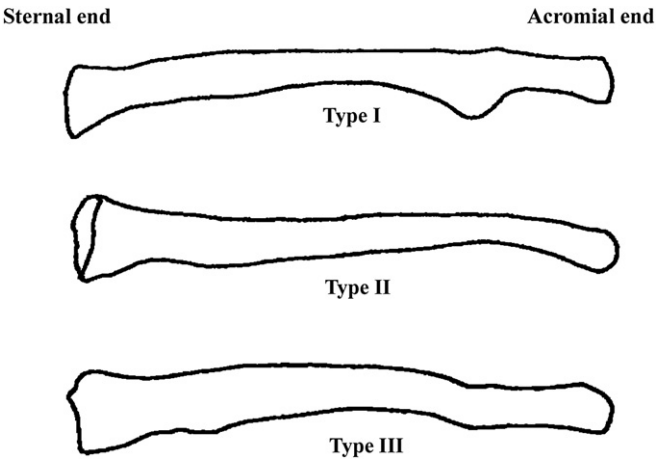

Fig. 3. The three types of modern human clavicle (see text for definition).

(Napier, 1965; Vandermeersch, 1991) so that the external curvature is underestimated. In contrast, the KNM-WT 15000 (left) clavicle is nearly complete (Walker and Leakey, 1993), and its scores may reflect a peculiar clavicular morphology in *Homo ergaster*. However, more clavicles belonging to *Homo ergaster* are needed to conclude that this morphology characterizes the species, particularly given that the KNM-WT 15000 *right* clavicle displays the modern human morphological pattern.

Curvatures in dorsal view

In dorsal view, modern human clavicles can be classified into three morphological groups (Fig. 3). The most common is Type I, according to the studies of Olivier (1951b,c, 1954a,b, 1955; Olivier et al., 1954) on more than 800 clavicles from Europe, Africa, America, and Australia. Type I clavicles possess only an inferior curvature. Type II clavicles are far less common, and display two curvatures in dorsal view—a superior one at the sternal end and an inferior one at the acromial end (Olivier, 1951b,c, 1954a,b, 1955; Olivier et al., 1954). Type III clavicles show a superior curvature at the acromial end but no curvature at the sternal end (Olivier, 1951b,c, 1954a,b, 1955; Olivier et al., 1954). Type III clavicles are by far the least common form (Olivier, 1951b,c, 1954a,b, 1955; Olivier et al., 1954).

All of the clavicles that do not belong to extant humans or Upper Paleolithic humans display two curvatures in dorsal view—an inferior one at their acromial extremity and a superior curvature at their sternal extremity (Fig. 4; Table 4). However, the Type II morphology of modern human clavicles, with two curvatures in dorsal view, is different from that of Neandertals and earlier *Homo*.

Table 3
Results of *t*-tests comparing the external and internal curvatures of Neandertal (Nd), modern human (MH), and Upper Paleolithic (UP) clavicles ($\alpha = 0.05$)

External curvature					Internal curvature				
	n	Mean	SD	Var		*n*	Mean	SD	Var
MH	33	16.115	2.645	6.995	MH	33	12.616	2.522	6.362
UP	23	16.055	3.053	9.320	UP	24	12.866	2.446	5.985
Sample difference			Significance test		Sample difference			Significance test	
DiffMean = 0.060			$t = 0.078$		DiffMean = −0.250			$t = -0.374$	
StErr = 0.765			df = 54		StErr = 0.668			df = 55	
Var = 7.942 (pooled)			$p = 0.9381$		Var = 6.205 (pooled)			$p = 0.7097$	
Nd	17	14.798	2.698	7.281	Nd	17	12.614	1.812	3.282
MH	33	16.115	2.645	6.995	MH	33	12.616	2.522	6.362
Sample difference			Significance test		Sample difference			Significance test	
DiffMean = −1.317			$t = -1.657$		DiffMean = −0.002			$t = -0.002$	
StErr = 0.795			df = 48		StErr = 0.690			df = 48	
Var = 7.091 (pooled)			$p = 0.1041$		Var = 5.335 (pooled)			$p = 0.9981$	

The superior curvature, when present, is less pronounced and less frequent in modern humans (Tables 5 and 6; Fig. 4). In some Neandertal clavicles (Régourdou left and right, La Ferrassie I right, Krapina 153 and 154) and in the Nariokotome specimens, the superior curvature is even more pronounced than the inferior one (Table 4), which is rarely, if ever, the case in modern human and Upper Paleolithic clavicles. However, three Neandertal clavicles (Kebara right and left and Krapina 143) display a modern morphology, showing only an inferior curvature. The peculiar morphology of these three clavicles might be explained by an east-to-west morphological cline (Voisin, 2004, 2006a, in press). In fact, in the western part of Neandertal range, all clavicles display two curvatures in dorsal view whereas in the eastern part, the morphology is modernlike. Between them, in central Europe, the modern and archaic morphologies both exist. There are few Neandertal clavicles, especially in the Levant, but similar morphological clines exist for many other cranial and postcranial traits (Voisin, 2006c, in press).

The Omo I clavicle displays two curvatures in dorsal view (Fig. 5; Table 4), and fits well within the range of variation of modern humans. In Olivier's (1951a) scheme, the Omo I specimen can be classified as a Type II clavicle. As Omo I also displays a superior curvature at the acromial extremity, fitting the modern and Paleolithic human range of variation (Table 7), it can be classified as Type III. The Type III morphology is far less common than the two others, but it has never been observed in other hominins, apes, or monkeys (Olivier, 1953; Voisin, 2000, 2006b). In other words, Type III clavicles might exist only in modern and Upper Paleolithic humans (Table 6).

Discussion

In cranial view, clavicles from *H. habilis* to modern humans do not show great differences. In particular, Neandertal clavicles are not more S-shaped than those of modern human, as had been previously asserted (Boule, 1911–1913; Patte, 1955; Heim, 1982a,b; Vandermeersch and Trinkaus, 1995). As shown by previous work (Voisin, 2000, 2004, 2006b), clavicular morphology in superior view is essentially related to the ability to elevate the arm (particularly in protraction because the pronounced internal curvature acts as a "crank," especially for the pectoralis major). This ability allows apes and humans not only to climb, but also to throw, carry, and manipulate heavy objects. In other words, the functional behaviors permitted by Omo I's shoulder would have been identical to that of other species of *Homo*.

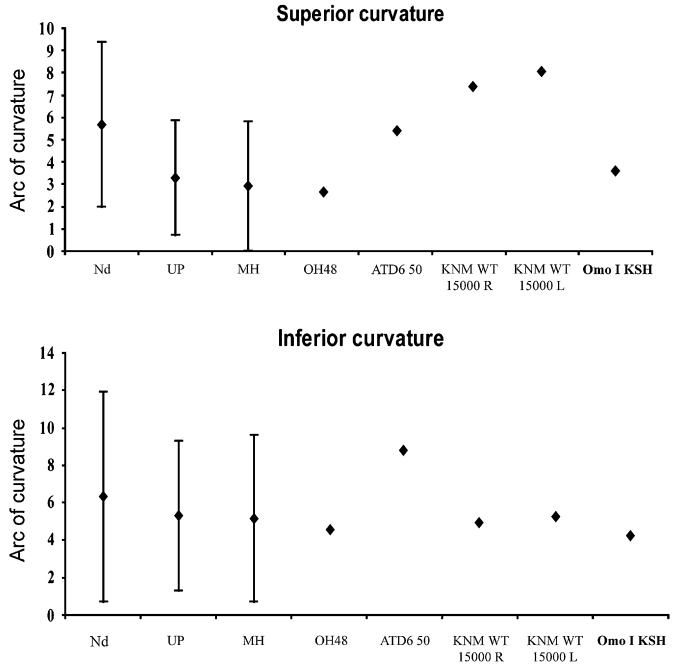

Fig. 4. Mean and range of variation of clavicle curvatures in dorsal view in *H. habilis*, *H. ergaster*, *H. antecessor*, Neandertals (Nd), Upper Paleolithic (UP) remains, and modern humans (MH). Only individuals with a superior curvature were retained for estimating means and standard deviations in modern humans and Upper Paleolithic remains.

Table 4
Values of the inferior and superior clavicular curvatures in Upper Paleolithic and other hominin remains

Individual	Inferior curvature	Superior curvature
Omo I KHS (L)	4.3	3.6
Upper Paleolithic		
Abri Pataud	6.9	0
Qafzeh 9 (L)	8.6	—
Taf V-6 (R)	5.8	0
Taf XXIII (L)	5.1	0
Taf XIX-3a (L)	3.7	3.5
Taf V-24 (L)	3.4	0
Taf XI-AR (R)	5.7	0
Taf XVa (L)	5.3	0
Taf XVc (L)	0	0
Taf XVII-26 (R)	6.0	0
Taf XVIII-6 (R)	4.6	0
Taf XIIIa (L)	3.9	0
Taf VIII-3bis (L)	10.7	0
Taf XXVa (R)	3.5	2.7
Taf IX-39 (L)	6.6	0
Taf XIIIb (R)	3.3	3.6
Taf XVIIa (R)	0	2.5
Taf XVI-15 (R)	4.5	3.1
Taf XVI (R)	6.3	3.3
Taf XIV (L)	0	0
Taf 24-5 (R)	3.1	0
Taf XIX-3 (R)	3.4	6.0
Taf XXVc (L)	0	1.5
Mean	**5.3**	**1.3**
Standard deviation	**2.0**	**1.8**
Neandertals		
Régourdou (R)	7.4	8.0
Régourdou (L)	3.0	3.2
Kebara (L)	4.9	0.0
Kebara (R)	3.4	0.0
La Ferrassie 1 (R)	5.4	5.8
La Ferrassie 1 (L)	8.2	2.6
Neanderthal (R)	7.4	6.2
Krapina 153 (L)	3.8	3.9
Krapina 142 (R)	6.9	5.9
Krapina 143 (R)	6.3	0
Krapina 154 (L)	6.3	6.6
Krapina 149 (R)	13.3	—
Krapina 145 (R)	—	7.2
Krapina 144 (R)	9.3	—
Krapina 155 (L)	6.8	Present
Krapina 156 (L)	2.2	—
La Chapelle-aux-Saints (L)	—	7.37
Mean	**6.3**	**4.4**
Standard deviation	**2.8**	**3.0**
Lower Paleolithic		
KNM-WT 15000 (R)	5.0	7.4
KNM-WT 15000 (L)	5.3	8.1
ATD6-50 (R)	8.8	5.4
OH 48 (L)	4.6	2.7

"Present" indicates that curvature is present but impossible to estimate because of the incompleteness of the bone; a dash indicates that the presence of curvature is impossible to assess because of the incompleteness of the fossil. The superior-curvature data correspond only to the sternal-end curvature, as defined in the methods section; in other words, no data for acromial superior curvature (Type III clavicle) are included.

Table 5
Results of *t*-tests comparing the inferior and superior curvatures of Neandertal (Nd), modern human (MH), and Upper Paleolithic (UP) clavicles ($\alpha = 0.05$)

Inferior curvature					Superior curvature				
	n	Mean	SD	Var		*n*	Mean	SD	Var
MH	33	4.982	2.373	5.631	MH	33	1.146	1.698	2.884
UP	24	4.362	2.666	7.109	UP	23	1.295	1.804	3.255
Sample difference			Significance test		Sample difference			Significance test	
DiffMean = 0.620			$t = 0.924$		DiffMean = −0.148			$t = -0.314$	
StErr = 0.671			df = 55		StErr = 0.473			df = 54	
Var = 6.249 (pooled)			$p = 0.3595$		Var = 3.035 (pooled)			$p = 0.7550$	
Nd	18	6.082	2.599	6.755	Nd	16	4.684	2.936	8.617
MH	33	4.982	2.373	5.631	MH	33	1.146	1.698	2.884
Sample difference			Significance test		Sample difference			Significance test	
DiffMean = 1.100			$t = 1.530$		DiffMean = 3.538			$t = 5.349$	
StErr = 0.719			df = 49		StErr = 0.661			df = 47	
Var = 6.021 (pooled)			$p = 0.1325$		Var = 4.714 (pooled)			$p < 0.0001$	

The superior-curvature data correspond only to the sternal-end curvature, as defined in the methods section; in other words, no data for acromial superior curvature (Type III clavicle) are included.

Table 6
Clavicle-type proportions

Group	Type I	Type II	Type III
Anatomically modern humans	60.9%	39.1%	30.4%
Extant humans	84.9%	15.1%	24.2%
Neandertals	21.4%	78.6%	0.0%

Some clavicles show both Type II and III morphologies, and thus the sum can be higher than 100%. "Anatomically modern humans" contains Upper Paleolithic specimens and Omo I.

On the other hand, two groups may be distinguished in dorsal view among clavicles in the genus *Homo*. The first is characterized by two pronounced curvatures and includes all *Homo* groups studied here (*H. habilis*, *H. ergaster*, *H. antecessor*, and Neandertals), except modern human and Upper Paleolithic remains (for discussion, see Voisin, 2004, 2006a). Clavicles of the second group show only the inferior curvature in dorsal view or two slight curvatures, and they belong solely to recent and Upper Paleolithic humans (Voisin, 2004, 2006a).

Clavicles with two pronounced curvatures in dorsal view, such as those of Neandertals, are associated with scapulae that sit high on the thorax (Voisin, 2004, 2006a,b). In contrast, clavicles with only one inferior curvature or two slightly pronounced curvatures are associated with scapulae that sit low on the thorax (Voisin, 2004, 2006a,b). As the Omo I clavicle displays two slight curvatures in dorsal view, it is predicted to be associated with a modern shoulder architecture, with the scapula positioned on the thorax similarly to that of Upper Paleolithic and more recent humans. Thus, Omo I was morphologically modern in clavicular morphology, and probably in shoulder architecture, while contemporaneous human groups, such as the Neandertals, remained more archaic in this respect. In dorsal view, the Omo I clavicle is very similar to those of Upper Paleolithic and modern humans, with some individuals from the latter group showing the rare Type III morphology (Olivier, 1951a) that is present also in Omo I. On the other hand, the Upper Paleolithic and Omo I clavicles are different from Neandertals, *H. antecessor*, *H. ergaster*, and *H. habilis* specimens because they do not display the pronounced double curvature in dorsal view (Voisin, 2004, 2006b).

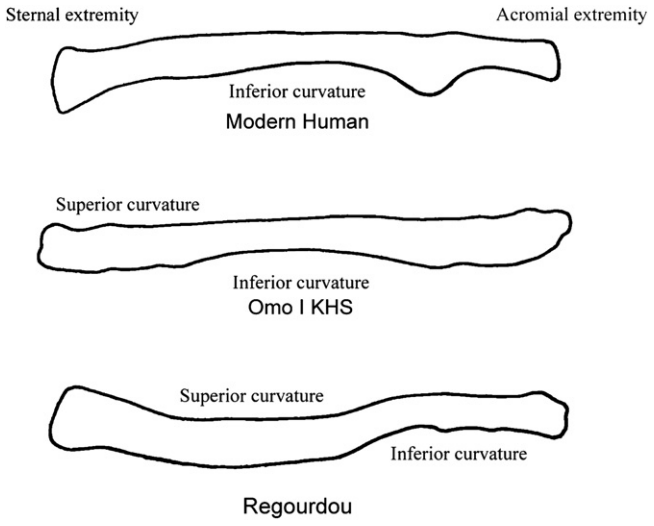

Fig. 5. Dorsal views of the clavicles of a modern human (top), Omo I (middle), and a Neandertal (bottom).

Conclusion

In cranial and dorsal view, the Omo I clavicle displays no significant differences from the clavicles of anatomically modern humans, including recent and Upper Paleolithic specimens. Because clavicular morphology allows one to infer major aspects of shoulder architecture and movements of the upper limb (Voisin, 2004, 2006a,b), Omo I's morphology shows that it likely possessed a shoulder architecture and capabilities for arm movements that were very similar to those of modern humans. The Omo I scapula probably sat low on the thorax, lower than in earlier *Homo* or in Neandertals, but in a position similar to that observed in modern humans.

The similarity between Omo I's shoulder girdle and that of modern humans confirms the conclusions of almost all studies that have been made on this skeleton since its discovery in 1967, reinforcing the conclusion that the specimen is both anatomically modern and the earliest example of an anatomically modern human currently known.

Table 7
Statistics for acromial superior curvature (i.e., values for the curvature characteristic of Type III clavicles)

Group	Mean	Standard deviation
Extant humans	3.45	1.56
Upper Paleolithic humans	3.64	1.43
Omo I	2.94	—

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